

Semispecies Relationships between *Heliconius erato cyrbia* Godt. and *H. himera* Hew. in Southwestern Ecuador

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Abstract. A suture zone between *H. erato cyrbia* and *H. himera* has been found in southwestern Ecuador. Presumably F_1 and at least F_2 hybrids have been captured, but their frequency is much lower than expected in the case of random mating and most individuals of the two parental taxa show no sign of hybridization. It is concluded that they behave as semispecies. The evolutionary significance of these observations is discussed.

Introduction

Very widespread in the neotropical region, *Heliconius* butterflies are the best studied in this area. Amongst them, the two muellerian mimics *H. erato* (L.) and *H. melpomene* (L.) have given rise to many detailed studies, both in the field of genetics (Turner and Crane, 1962; Sheppard, 1963; Emsley, 1964; Turner, 1972) and that of evolutionary systematics (Emsley, 1965; Brown, Sheppard & Turner, 1974; Brown, 1979).

The taxonomical situation of *H. erato* is especially complex in Ecuador, where the species is represented by ssp. *lativitta* Btlr. in the Northern part of the Amazonian lowlands and ssp. *etylus* Salv. in the southern part of the same region. The two taxa are very much alike. On the contrary, in the upper part of the Pastaza valley, ssp. *notabilis* Salv. and Godt. flies and looks extremely different. However, *lativitta* and *notabilis* interbreed freely in the transition region, giving rise to all possible intermediate and recombined phenotypes (Descimon & Mast de Maeght, 1971). On the Pacific slopes, the species is represented by ssp. *cyrbia* Godt., which is strikingly distinct from the Amazonian subspecies. The continuity of the specific complex was demonstrated by Emsley (1964, 1965), both through laboratory crosses and biogeographical studies.

The taxonomic status of *H. himera* Hew. is less well understood. This taxon is endemic to southern Ecuador and adjacent Peru, associated with

dry forest and semi-arid conditions. When we wrote our article about the *Heliconius* of Ecuador in 1971, we quoted that species from Rio Engano, a small stream running down from the Cerro de Abitagua, near Puyo. Actually, we were misled by a synonym: there is another rio of this name in southern Ecuador—in Spanish, Engano means “error”!. Thus, the quotation of *H. himera* from the Pastaza region is a mistake and all the considerations developed in our paper are irrelevant. In fact, fifteen days after it was published, we became aware of the real ecology of the butterfly, which we observed in great numbers in the region of Jaen, Amazonas, northern Peru, together with many of the characteristic endemics of the “Maranon dispersion center” (Mueller, 1973), such as *Battus streckerianus* Honr., *Diaethria ceryx* Hew. and many more. Even though Brown (1979) cited some localities where either *cyrbia* or *etylus* are reported together with *himera*, no data were provided about the form of the contact. Thus, the taxonomic structure of the *erato* complex is uncertain in southern Ecuador; Lamas (1976), quoting unpublished data of Brown, Benson, Gilbert and Lamas, as well as Brown (1979), consider *erato* and *himera* as conspecific, but without presenting facts. Moreover, it was not specifically stated whether the oriental or the occidental populations of *erato* are considered.

The southern region of Ecuador is unique in all the Andes in that the Cordillera is sufficiently low to allow faunal exchanges. It was this phenomenon that we intended to study in our 1971 travel in northern Peru. Actually, we were bitterly disappointed, because faunal exchanges between the lowland moist forest regions of both sides are hindered by the presence of an extensive semi-arid zone, the above mentioned “Maranon center”, which acts as an efficient barrier.

The dry forest faunas fly on both sides of the watershed and penetrate (at least partially) the basin of the Rio Catamayo and that of the Rio Tumbes. In the upper part of the latter (Rio Puyango), a very clearcut contact between an extensive area of dry forest and a tongue of moist premontane forest was observed in January 1975 by H. Descimon. This zone is cut by the road Loja-Catamayo-Portovelo ca 8 km above the small village of Guayquichuma, at an elevation of 1200-1400 m. The zone is also clearly detectable on the very good ecological map of the Atlas del Ecuador (1982). In that locality, a single *Heliconius* was seen, flying at the bottom of an inaccessible glen, which looked like a *cyrbia* x *himera* hybrid. In spite of some efforts, it could not be secured, and no other individual be found in the neighbourhood.

In July 1982, the authors, together with F. Lafite and H. D.’s family, undertook a journey to southern Ecuador, one of the main objectives of which was to clear up the *himera-cyrbia* problem. The Rio Puyango locality had not changed; two small valleys separated by ca. 2 km were explored and were actually the only two accessible biotopes with some remnants of

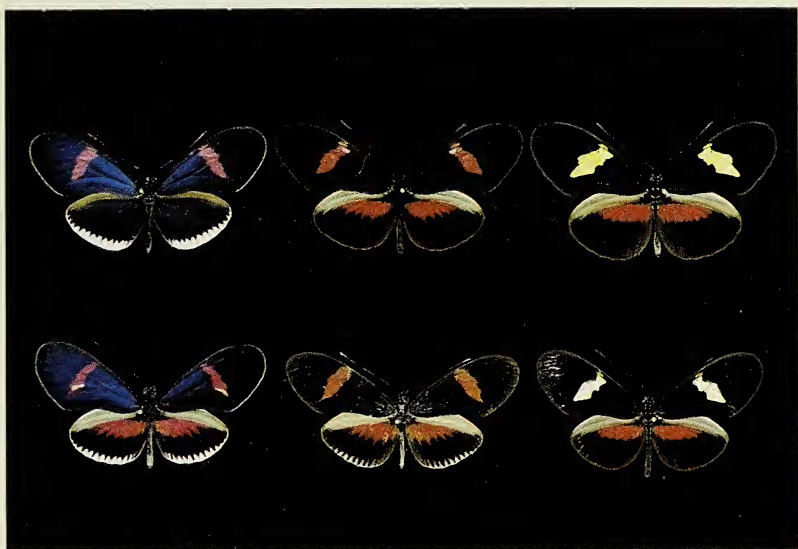


Fig. 1. *Heliconius* from southwestern Ecuador

1. *H. erato cyrbia*, male. Guayquichuma, Dept. el Oro, 200782. 2. *H. "lafitei"* (*himera* x *cyrbia*), same locality, 190782 (No. 1). 3. *H. himera*, same locality, 200782. 4. *H. "clarae"* (probably "*lafitei*" x *cyrbia*), same locality, 200782 (No. 4). 5. *H. "clarae"*, same locality, 210782 (No. 5). 6. *H. "petri"* (probably "*lafitei*" x *himera*), same locality, 190782 (No. 6).

forest. Both upwards and downwards along the road, all slopes become dryer and degraded, and the moist forest disappears.

All over western Ecuador, *H. erato cyrbia* was on the wing, while *H. melpomene* was very scarce—a fact in contradiction with our previous assumptions (Descimon & Mast de Maeght, 1971) and the widespread opinion that *H. melpomene* is commoner than *H. erato*. An explanation would be that *H. erato* flies more during the dry season and *H. melpomene* more during the rainy season, in western Ecuador at least—a possibility that should be checked by more numerous observations.

The first *Heliconians* to be seen in the Guayquichuma glen were typical *cyrbia*, but a *himera* was readily observed in the same place. Then, three hybrids were caught successively by F. Lafite. A total of 31 pure *cyrbia*, 11 *himera* and 6 hybrids were caught by the six collectors and in three days of serious efforts. All hybrids were males.

Description

The hybrids fall into three clearcut categories. Their main characteristics, compared with those of the parent butterflies are given in Table 1 and illustrated in Figure 1. Since giving Linnean names to hybrids is not allowed by the International Code of Zoological Nomenclature, we will

Table 1. Comparative features of *Heliconius erato cyrbia*, *H. himera* and of their hybrids from South-western Ecuador.

	Upside background	FW upside transverse band	HW upside "dennis" bar	HW upside white margin	HW underside bar
<i>H. erato cyrbia</i>	vivid blue iridescence	red, distal, narrow	absent	white with black veins	yellow
<i>H. himera</i>	black	greenish yellow, wide	red, large, almost straight distad	absent	absent, some dull red scales
hybrid "lafitei"	raven blue-black iridescence	red with few anterior white scales, intermediate shape	red, large, somewhat serrate distad	absent	absent, dull red scales
hybrid "clarae"	vivid blue iridescence	as in <i>cyrbia</i> , with a few posterior white scales	red, large, serrate distad	white, with prominent veins	very large, red basad white distad
hybrid "petri"	black	white slightly tinged yellow, anterior red scales	red, large, a little serrate	absent	absent, dull red scales

designate them by mere "nicknames", which will honor our young and enthusiastic companions Frederic Lafite, Pierre Descimon and Claire Descimon.

a. *H. erato cyrbia* x *himera* "lafitei"

Deep blue background, forewings upperside with a transverse band, red with a few anterior white scales, a red band on the upperside of hindwings, which have no white margin. No. 1, 8 km above Guayquichuma, dept el Oro, Ecuador, 1200 m, 190782, F. Lafite leg.; No. 2, same date; No. 3, 10 km above Guayquichuma, 1250 m, 200782, J. Mast de Maeght leg.

b. *H. erato cyrbia* x *himera* "clarae"

Mostly alike *H. erato cyrbia*, but with a large red transverse ("dennis") band on the hindwing upperside; this band is more serrate distally than in *H. himera*. On the underside, the hindwing transverse bar is large, red basally and white distally, a feature that is not observed in any other form. No. 4, 10 km above Guayquichuma, 1250 m, 200782, H. Descimon leg. No. 5, same locality, 210782, same collector. This individual has a white marginal band darkened by black scales.

c. *H. erato cyrbia* x *himera* "petri"

Mostly like *himera*, but the forewing transverse band white with only a very faint yellow tinge and a border of red scales, mostly distal. 8 km above Guayquichuma, 190782, No. 6, F. Lafite leg.

Except for individual No. 3, all insects are in H. Descimon's coll. and will be given to the Museum National d'Histoire Naturelle in Paris. No. 3 (coll. J. Mast de Maeght) will be given to the British Museum.

Discussion

When two parapatric taxa show a contact zone, it is generally possible to determine whether they are mere subspecies of a single species, or belong to two distinct specific units.

In the first case, a "hybrid zone" (Short, 1969) is observed, with a complete blending of the genetic pools. Such a case is indeed observed in the populations of *H. erato notabilis* and *H. erato lativitta* of the lower Pastaza region. In the second case, no actual genetic exchange takes place and the two populations remain completely distinct, even if F₁ hybrids casually occur with a noticeable frequency.

However, less clearcut situations are often noticed ("suture zones" of Remington, 1968), where a limited gene exchange is observed: both taxa remain distinct, with a restricted amount of intermediates, which are not limited to F₁ hybrids. Such taxa, neither species nor subspecies, are usually designed by the term "semispecies"—though Bernardi (1980) has clearly demonstrated that the correct name applying to these relations is "quasispecies"—it must be added that this taxon is considered by

Bernardi as *intraspecific*.

In the present case, it is possible to assume, with a reasonable certainty, that the three butterflies designed under the nickname "lafitei" are F_1 hybrids. They are indeed approximately intermediate between *H. erato cyrbia* and *H. himera*, and especially so by phenetic characters such as the background color and the shape and position of the forewing transverse band. The other characters fit also well with what is known about their inheritance, thanks to the work of Emsley (1964) on the crossing of *H. erato cyrbia* and *H. erato adanusa*. On the contrary, it is hard to assign also "clarae" and "petri" to F_1 hybrids. The former would better correspond to a backcross "lafitei" \times *erato cyrbia* and "petri" to a backcross "lafitei" \times *himera* or even to an almost typical *H. himera* with a few *erato cyrbia* genes.

In the absence of laboratory crosses, these assignments remain of course tentative, but we believe that they are far the most likely. They would suggest that the F_1 hybrids are not sterile and thus that there is not a complete barrier of genetic incompatibility between *H. erato cyrbia* and *H. himera*.

It is clear that, in the restricted area where we have met them together, both taxa do not behave as mere subspecies. Would they have done so, a thorough gene exchange would have produced many more intermediates than observed. For instance, in the conditions of a stationary equilibrium and assuming constant the proportions of the parents in the previous generation, a neutral homogamy situation would have produced 25 *erato cyrbia*, 3 *himera* and 17 "lafitei" (if these are assumed to be F_1 hybrids), instead of 31, 11 and 3, respectively observed ($X^2 = 33$, $P < 0.01$). Thus, already at the level of F_1 hybrid production, at least some of these prerequisites are not present. One may add that the number of "clarae" and "petri" is also inferior to that expected for backcrosses assuming the frequency of *erato cyrbia*, *himera* and "lafitei" to be constant (5 and 2 instead of 2 and 1 observed).

It is also difficult to assume *H. erato cyrbia* and *H. himera* to be fully distinct species. In this case, indeed, hybrids would have been at least rarer and limited to F_1 —hybridization not implying gene exchange (Bigelow, 1965). So, no matter the mechanisms leading to this situation, both taxa should be considered as "semispecies" (*sensu* Lorkovic, 1955, and not *sensu* Mayr, 1940).

Such situations are always distressing both to systematicians and to geneticists. It is hard to conceive why hybridization, even limited, does not lead to a complete blending of the gene pools. In the present state of affairs and in practically all the known "semispecies" cases, the answers remain speculative. Moreover, laboratory results may by no means always be transposed to natural situations.

A first class of explanation commonly put forward is ecogeographical: the two taxa "brush each other" in much too restricted an area to produce

an equilibrium; their phenology and habitat choice do not allow the cohabitation to be more than episodic; the meeting of the populations is too recent to have produced either a fusion of the gene pools or a selective elimination of the illegitimate mating tendencies. "Semispecies" would thus be often man-made artefacts, resulting from the destruction of natural barriers (Woodruff, 1973). Such arguments appear somewhat relevant in the present case; one may only object that hybridization occurred already 7 years ago and during the opposite half of the year. In the cohabitation zone, the extent of which is possibly much larger than was actually explored, the two taxa were intimately mixed.

A second type of explanation involves some kind of impairment of the selective value of the hybrid phenotypes. Concerning "muellerian protection", which might be lowered in hybrids, it must be noted that this factor does not hinder an active gene exchange in other "hybrid belts", such as that of the Pastaza, for instance. Altered physiological viability of hybrids between a taxon mainly adapted to wet forest and another one adapted to semi-arid forest, "hybrid breakdown" (Oliver, 1979), lower efficiency in mating and sexual attraction, partial sterility are among the most obvious factors which are usually quoted.

As Bernardi (1980) stressed, the study of "semispecies" (quasi and vicespecies, according to the terms he and ourselves consider correct) is of strategic importance to clear up the mechanisms of speciation. However, in the present case, and though *Heliconius* are becoming the best genetically known butterflies, one may cast doubts about the observational and experimental facilities offered by populations flying in remote parts of southern Ecuador, while it is already difficult to reach conclusive evidences in more accessible countries.

The only somewhat feasible and significant approach to the problem may be provided by electrophoretic analysis, which would afford much more refined data about the actual gene flow between both populations and their degree of divergence.

Otherwise, it would of course be very interesting to carry out comparative studies upon a possible (and probable) contact between *H. himera* and *H. erato etylus* in the eastern region.

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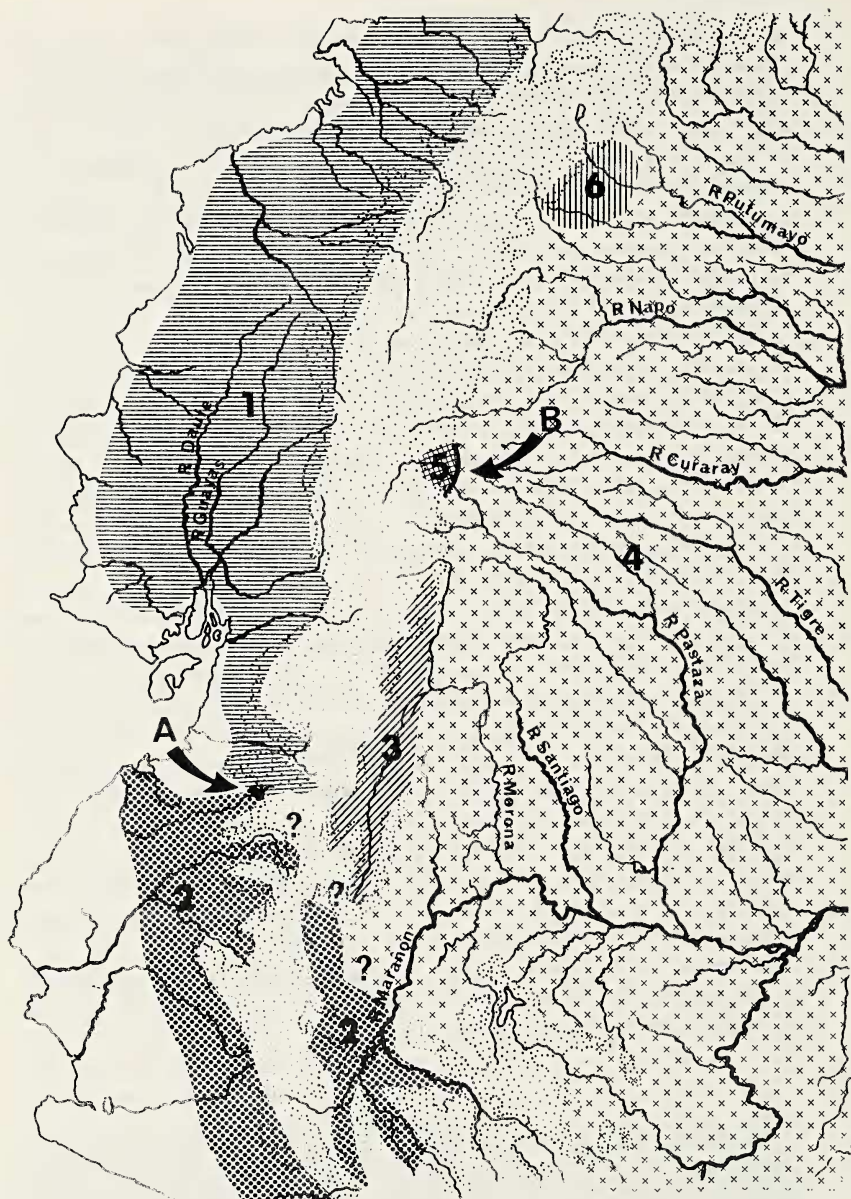


Fig. 2. Distribution of the subspecies and semispecies of *Heliconius erato* in Ecuador and the adjacent regions of Peru and Colombia.

1. *H. erato cyrbia* 2. *H. himera* 3. *H. erato etylus* 4. *H. erato lativitta*
 5. *H. erato notabilis* 6. *H. erato dignus* A. Suture zone of Guayquichuma
 B. Hybrid belt of the Pastaza region.

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